Euphytica **107:** 71–78, 1999.

Inheritance and allelism for resistance to Russian wheat aphid in an Iranian spring wheat

B. Ehdaie[1] & C.A. Baker[2]
[1] *Dept. of Botany and Plant Sci., Univ. of California, Riverside, CA 92521-0124, U.S.A.;* [2] *USDA-ARS, 1301 N. Western St., Stillwater, OK 74075, U.S.A.*

Received 10 April 1998; accepted 4 January 1999

Key words: Russian wheat aphid, resistance, inheritance, allelism, segregation ratio, wheat, *Triticum aestivum* L.

Summary

Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko), is an important pest of wheat (*Triticum aestivum* L.) in the United States of America. Developing adapted wheat cultivars with genetic resistance to RWA is an effective control strategy. Genetic studies were conducted to determine the mode of inheritance of gene(s) conferring resistance to RWA in an Iranian landrace wheat line, G 5864. For the inheritance study, G 5864 was crossed with the susceptible wheats 'Yecora Rojo' and ND 2375. Seedlings of F_1, reciprocal F_1, F_2, BC_1 to the susceptible parent (BCS), and BC_1 to the resistant parent (BCR) were screened for RWA reaction. Several phenotypic segregation ratios were tested in the F_2 populations for goodness of fit; the 9 : 3 : 3 : 1 ratio (resistant: rolled leaves: stunted plants: susceptible) was an acceptable fit in all cases. Thus, resistance in G 5864 seemed to be controlled by two independent dominant genes with additive gene effects. The allelic relationships of gene(s) in this line with genes in other resistant lines, PI 137739 (*Dn1*), PI 262660 (*Dn2*), PI 372129 (*Dn4*), PI 294994 (*Dn5*), and PI 243781 (*Dn6)*, were also studied. Segregation patterns observed in G 5864 $\times$ resistant (R $\times$ R) F_2 populations were inconclusive. However, no susceptible plants were observed in these F_2 populations. If previous reports concerning the number of resistance genes present in the other resistant lines are correct, then given the high manifestation of resistance observed in G 5864, and given the absence of susceptible plants in the R $\times$ R F_2 populations, it is indicated that RWA resistance in G 5864 is either controlled by different alleles at the same loci as the other resistance genes, or that G 5864 shares a resistance gene with each of the other resistant lines.

Abbreviations: RWA, Russian wheat aphid. BCS, backcross to susceptible parent. BCR, backcross to resistant parent

Introduction

Russian wheat aphid first appeared in North America in Mexico in 1980 and has become an economically important pest of wheat and barley. The aphid is believed to have spread from western Asia to the United States and Canada via South Africa and Mexico (Smith et al., 1991). Since its subsequent detection in Texas in 1986 (Stoetzel, 1987), RWA has been found in 17 western U.S. states and several Canadian provinces and, by 1994, had caused economic losses in excess of $986 million (C. Patrick & D. Legg, 1998, personal communication).

Screening of germplasm originating from the area where RWA is endemic has identified many lines showing some level of resistance. Genetic resistance to RWA was first reported from South Africa in the wheat accessions PI 137739 (from Iran) and PI 262660 (from the former Soviet Union) (Du Toit, 1987, 1988). Seedling resistance in PI 137739 and PI 262660 was reported to be controlled by the dominant genes *Dn1* and *Dn2*, respectively (Du Toit, 1989).

In the United States, the first significant level of resistance to RWA in wheat was found in Colorado in PI 372129 (from the former Soviet Union) (Quick et al., 1991). The resistance gene in PI 372129 appeared

to differ from *Dn1* and *Dn2* on the basis of resistance mechanisms (Meyer et al., 1989), and it was designated as *Dn4* on the basis of an allelism test (Saidi & Quick, 1996). A fourth resistant wheat accession, PI 294994 from Hungary, was identified in 1987 by Du Toit (1988). Seedling and adult plant reactions initially indicated that resistance in PI 294994 was controlled by two genes: a dominant allele at one locus and a recessive allele at the second locus (Elsidaig & Zwer, 1993). However, Marais & Du Toit (1993) reported that resistance in this line is controlled by a single dominant gene and proposed the symbol *Dn5* to designate the dominant allele in PI 294994. In support of these differing reports, Zhang et al. (1997) studied genetic variation in PI 294994 and reported that the number of resistance genes in the original individual plants were different. The authors regrouped the original PI 294994 wheat accession into at least three sub-accessions based on resistance to RWA. A fifth resistant wheat accession, PI 243781 from Iran, was reported in 1989 (Quick, 1989). Resistance in this accession was reported to be controlled by a dominant gene designated as *Dn6* (Saidi & Quick, 1996). Each of the studies which reported a single RWA-resistance gene primarily based their conclusions on F_2 segregation ratios.

An allelic study conducted recently indicated that PI 294994 had at least one RWA-resistant gene in common with PI 137739, PI 262660, PI 372129, and PI 243781, and that *Dn4* and *Dn6* were not allelic with each other or with *Dn1* or *Dn2* (Saidi & Quick, 1996). However, this study suggested that contrary to an earlier report, *Dn1* and *Dn2* were allelic. Monosomic analysis indicated that *Dn1* and *Dn5* (in PI 137739 and in PI 294994, respectively) were located on chromosome 7D (Schroeder-Teeter et al., 1994; Marais & Du Toit, 1993). Since these studies were all conducted prior to the research showing the presence of different resistant genotypes in the PI 294994 accession, it is unclear which 'sub-accession' of PI 294994 was used in these studies.

Control of RWA is complicated by the leaf-rolling symptom of infestation that protects the aphid colonies and reduces the efficacy of chemical control. Development of resistant cultivars by transferring simply inherited resistance genes to adapted cultivars is the most effective method of controlling this pest in small grains. Unfortunately, most of the resistant accessions are of poor agronomic quality (Quick et al., 1991; Baker et al., 1992), and extensive backcrossing is needed to get RWA resistance into an agronomically acceptable background.

The symptoms of RWA damage and the presence of the aphid itself were first detected on wheat plants in experimental plots at the Moreno Farm (Moreno Valley) of the University of California, Riverside, Agricultural Experiment Station (UCRAES) in the 1989–90 season. In 1991, most of the wheat cultivars planted at the station showed severe symptom development, including leaf rolling with moderate to heavy white streaking. The exceptions were lines collected from an Iranian landrace population that maintained flat leaves (no leaf rolling) and only developed very small and faint chlorotic flecks (no leaf streaking) with RWA infestation. The objectives of this study were to determine the inheritance of resistance in one of the lines, G 5864, belonging to this landrace population, and to determine the allelic relationships of these resistance gene(s) with other known genes.

Material and methods

Inheritance

Landrace populations of wheat collected from various localities of Balochestan Province, located in southeastern Iran, were planted separately at the South Coast Research and Extension Center (Irvine) of the University of California AES in the 1988–89 growing season. Seeds from each landrace population were space-planted, and single plants differing in morphological characters, such as date to maturity, plant height, spike length, spike color, and laxness were collected to represent different plant types existing within each of the landrace populations. Seeds from each collected plant were sown separately in the 1990–91 growing season at the UCRAES Moreno Farm. The offspring from a single plant were homogeneous for different morphological characters and thus were assumed to represent a pure line. In this season, the experimental plots were heavily infested with RWA, and most wheat cultivars and lines were severely damaged, except lines from a landrace population which had flat leaves with very small chlorotic specks. Subsequent evaluation of these lines under controlled infestation in 1992 in the glasshouse at UCR and at the Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID (M.M. Rafi, personal communication), confirmed the high degree and homogeneous nature of resistance to RWA in one of these lines, designated as accession no. G 5864, UCR Germplasm

Collection, at both seedling and adult plant stages. In 1993, crosses including reciprocals, were made between resistant line G 5864 and two susceptible wheats, Yecora Rojo and ND 2375. In 1994, backcross populations (BCS and BCR) were produced for the G 5864 × Yecora Rojo and G 5864 × ND 2375 crosses, and the corresponding F_2 population was produced for each of the crosses by selfing some of the F_1 plants produced in the previous year. The parents (between 86 and 166 individual plants of each parent line were screened), F_1 and reciprocal F_1 (55–59 plants were screened from each cross), backcross (36–58 plants were screened from each backcross), and F_2 populations (each population contained 388–389 plants) were used to determine the mode of inheritance of RWA resistance in G 5864.

Allelism

Seeds of known resistant accessions PI 137739 (*Dn1*), PI 262660 (*Dn2*), PI 372129 (*Dn4*), PI 294994 (*Dn5*), and PI 243781 (*Dn6*) were provided by Dr A. Saidi, Department of Agronomy, Colorado State University, Fort Collins, CO. Each of these accessions was crossed to G 5864 in 1994 or in 1995 to produce F_1 seeds; F_2 seeds were produced the next year by selfing F_1 plants. The F_2 plants (255–362 plants per population) were used to study allelic relationships among these resistant accessions.

Symptom expression and classification

Seedling resistance tests were conducted at the USDA-ARS facility in Stillwater, OK, in October–December 1995 and 1996. Tests were conducted under ambient light at 15–22 °C in greenhouse flats (35 × 51 × 9 cm) with a susceptible check wheat ('Karl 92' or 'Custer') planted in the outer rows and the appropriate susceptible parent in every third row to enable an accurate assessment of aphid distribution and ensure that infestation within a flat was uniform over time. Seeds were planted in 35-cm rows, 10 rows per flat, 30 seeds per row.

Seedlings were infested at the one-leaf stage, with approximately 10 RWA per plant according to the technique previously described by Webster (1990), which involves laying RWA-infested leaves between the rows. Aphids were obtained from colonies that were initiated from equal proportions of aphids collected in 1992 in Colorado, Idaho and Oregon. The colonies have been maintained on 'Wintermalt' barley (*Hordeum vulgare* L.); there has been no evidence of problems arising from transferring the aphids from barley to wheat in any of our screening tests. Flats were monitored daily to ensure even aphid distribution within a flat. Seedlings were infested for 3 weeks prior to rating.

Rather than grouping plants according to the standard RWA damage scale of 1–9 (Webster et al., 1987), rating scales were devised only after visual observation of the actual range of symptom development within each population. It is often the case that a population will not contain all of the categories described by the nine-point scale, and plants will often have symptom development that does not fall into one of the nine categories. Rejection of the standard rating scale may make it difficult to compare different populations, but it was felt that classification based on the actual range of symptoms within a population was more informative and allowed for better identification of intermediate classes. After visual observation of the four separate populations, it was determined that a single rating scale was appropriate for all populations. Damage ratings were divided into four classes.

R = resistant reaction similar to majority of G 5864; turgid, flat green leaves; no streaking or rolling; no stunting; no generalized chlorosis, may have slight leaf flecking,

Ml (rolled) = turgid green leaves with loose rolling; little or no stunting; may have slight streaking along midrib,

M2 (stunted) = turgid, flat leaves; stunted plants; may have some chlorotic streaking (this is a low level of resistance similar to that found in PIs 137739 and 262660),

S = tightly rolled leaves; heavy white streaking, especially along midrib; typical reaction of susceptible parent.

Counts of seedlings falling within the different damage classes were done when the susceptible parent showed severe streaking and tightly rolled leaves. Few plants within the susceptible lines were dead at time of rating. An effort was made not to classify plants simply as 'resistant' or 'susceptible' since there is usually a range of reaction within both of these categories and an early grouping of plants into only two classes limits analysis of possible gene action models.

Statistical analyses

The data of F_2 populations derived from crossing G 5864 to each of the susceptible parents were tested for goodness of fit to four phenotypic segregation

Table 1. Seedling reaction to Russian wheat aphid among bread wheat parents and their F_1, reciprocal F_1, and BCR progeny in seedling screening tests

Parents and progeny	Seedling reaction					
	Expected			Observed		
	R[a]		S	R		S
	no.					
G 5864	1	:	0	166[b]	:	0
Yecora Rojo	0	:	1	0	:	95
ND 2375	0	:	1	0	:	85
G 5864 × Yecora Rojo						
F_1	1	:	0	58	:	0
Reciprocal F_1	1	:	0	59	:	0
BCR (F_1 × G 5864)	1	:	0	57	:	0
G 5864 × ND 2375						
F_1	1	:	0	57	:	0
Reciprocal F_1	1	:	0	55	:	0
BCR (F_1 × G 5864)	1	:	0	58	:	0

[a] R = resistant; S = susceptible.
[b] Total number of G 5864 plants in the segregation studies involving crosses of G 5864 to each of the susceptible parents.

ratios, including: 3R (R + M1): 1S (M2 + S), 9R: 3M1: 3M2: 1S, 36R: 10M1: 12M2: 6S (derived on the basis of a three-gene epistatic model), and 9R: 6M (M1 + M2): 1S. For each of the BCS populations, the corresponding ratio, namely 1 : 1, 1 : 1 : 1 : 1, 1 : 2 : 2 : 3, and 1 : 2 : 1, was tested for goodness of fit. The individual chi-square (χ^2) for goodness of fit was calculated for each F_2 and for each backcross population, and a χ^2 was calculated on the basis of totals over F_2 crosses and over backcrosses (Steel & Torrie, 1980). The homogeneity χ^2 was also calculated to test the similarity of segregation over crosses.

Results and discussion

Inheritance

All seedlings of G 5864 were highly resistant, and those of Yecora Rojo and ND 2375 were susceptible to RWA (Table 1). The F_1 hybrids, including reciprocals, were highly resistant, indicating complete dominance of resistance over susceptibility, with no apparent cytoplasmic effect. These results were confirmed by BCR populations in which all individuals were highly resistant (Table 1). All known sources of resistance to RWA are conferred by dominant genes, with the possible exceptions of a recessive gene in PI 294994 wheat (Elsidaig & Zwer, 1993) and a single recessive gene, *Dn3*, in an accession of *Aegilops tauschii* Coss. (Nkongolo et al., 1991). Results from reciprocal crosses in spring barley also indicated absence of a cytoplasmic effect on plant response to RWA (Robinson et al., 1992).

The 3R : 1S F_2 ratio and corresponding 1 : 1 BCS ratio were included in order to demonstrate the ease with which plants in different resistance categories can be grouped into fewer categories, and so fit alternate gene models. The individual χ^2 calculated for the F_2 progeny derived from G 5864 × Yecora Rojo had an excellent fit to the 3R : 1S ratio (0.06, $P = 0.83$), while the χ^2 for the F_2 progeny from G 5864 × ND 2375 (2.592, $P = 0.11$) had a poorer fit to a 3R : 1S ratio, but was still within the acceptable range. The homogeneity χ^2 (0.944, $P = 0.36$) for the 3 : 1 ratio in the F_2 populations (Table 2) was also within the acceptable range, although the probability value ($P = 0.36$) was relatively low when compared with the other homogeneity χ^2 values. Therefore, a single-gene model could be an acceptable conclusion if it could be determined that grouping the four distinct categories into only two categories was a valid option. However, the M1 category does not have the extremely high level of resistance seen in the R category and should not be considered as highly resistant. The M2 category does not have the classic symptom development of the S category (tight leaf-rolling with heavy midrib streaking) and should not be considered susceptible. It must be remembered that the resistant PIs 137739 and 262660 both exhibit the M2 intermediate level of resistance and have both been used successfully in the development of RWA-resistant germplasm in many wheat breeding programs around the world. Therefore, plants with this lower level of resistance should not be grouped in the susceptible category.

The homogeneity χ^2 for the other three segregation ratios in F_2 populations and in the BCS populations were high (ranged from $P = 0.70$ to 0.98), indicating the similarity of samples taken from the F_2 populations and BCS populations across the two crosses. These observations allowed us to calculate χ^2 based on totals (Table 2), which is more powerful than the individual χ^2 to detect a small departure from the three hypothesized ratios (Steel & Torrie, 1980). The χ^2 based on totals for the phenotypic segregation ratio of 9 : 6 : 1 in F_2 progeny (4.62) was significant at $P = 0.10$, and that for 36 : 10 : 12 : 6 ratio in BCS progeny (8.34) was significant at $P = 0.03$ (Table 2).

Table 2. Segregation for resistance to Russian wheat aphid in bread wheat F_2 and BCS progeny in seedling screening tests

Progeny	Observed				χ^2 value at expected ratio							
	R[a]	M1	M2	S	3 : 1[b]	*P*	9 : 3 : 3 : 1	*P*	36 : 10 : 12 : 6	*P*	9 : 6 : 1	*P*
F_2	– no. of plants observed –											
G 5864 × Yecora Rojo	219	70	67	32	0.06	0.83	3.04	0.40	2.43	0.49	2.98	0.23
G 5864 × ND 2375	213	65	80	31	2.59	0.11	3.54	0.33	1.95	0.59	2.00	0.39
Total	432	135	147	63	1.70	0.21	5.15	0.18	2.29	0.47	4.62+	0.10
Homogeneity χ^2					0.94	0.36	1.34	0.70	1.47	0.69	0.32	0.85
BCS					1 : 1	*P*	1 : 1 : 1 : 1	*P*	1 : 2 : 2 : 3	*P*	1 : 2 : 1	*P*
F_1 × Yecora Rojo	12	13	12	17	0.30	0.61	1.26	0.74	4.79	0.19	1.22	0.55
F_1 × ND 2375	8	10	7	11	0.00	1.00	1.11	0.77	3.74	0.29	0.61	0.74
Total§	20	23	19	28	0.18	0.70	2.17	0.54	8.34	0.03∗	1.82	0.42
Homogeneity χ^2					0.12	0.74	0.19	0.98	0.19	0.98	0.01	0.98

[a] R = resistant; M1 = loosely rolled leaves; M2 = stunted plant, may have chlorosis; S = susceptible.
[b] Resistant (R + M1): susceptible (M2 + S).
+,∗ Significant at the 0.10 and 0.05 probability level.
§ Degrees of freedom for χ^2 based on totals and homogeneity χ^2 of F_2 and BCS progeny for 3 : 1 were 1 and 1, for 9 : 3 : 3 : 1 were 3 and 3, for 36 : 10 : 12 : 6 were 3 and 3, and for 9 : 6 : 1 were 2 and 2, respectively.

These observations suggest that the phenotypic segregation ratios of 32 : 10 : 12 : 6 and of 9 : 6 : 1 were not appropriate to explain the observed segregations in either F_2 or BCS populations.

The only phenotypic ratio that appeared to satisfy the individual χ^2s and the χ^2s calculated based on totals both for the F_2 and BCS populations was the 9 : 3 : 3 : 1 ratio (Table 2). The homogeneity χ^2s and probability values for the F_2 (1.34, 0.70) and BCS (0.19, 0.98) populations indicate an excellent fit to this segregation ratio. This ratio, which best accounts for all observed classes and gives a relatively more consistent fit in both the F_2 and BCS populations derived from the two crosses, suggests that RWA resistance in G 5864 is conditioned by two independent, completely dominant genes, AABB, with additive effects. Thus, the genotypic constitution of the highly resistant plants, the intermediate plants M1 and M2, and the susceptible plants in the F_2 progeny derived by crossing G 5864 (AABB) to a susceptible parent (aabb) was probably A_B_, A_bb, aaB_, and aabb, respectively.

Allelism

In the allelism test, each of the F_2 populations derived from crossing resistant accessions to G 5864 segregated for different resistance levels, but without the appearance of susceptible plants (Table 3). Classification of segregation in these F_2 populations was difficult, and the segregation ratios for the two- and three-gene segregation models did not fit the observed segregation patterns. In a cross between two resistant parents, the appearance of susceptible plants in the F_2 population would indicate that the parents have resistance genes that are nonallelic. Lack of appearance of susceptible plants in these same crosses might indicate that the two parents are carrying resistance gene(s) that are allelic, or that there are numerous genes involved. If numerous genes are involved, then the appearance of susceptible plants requires that an unusually large F_2 population be tested, especially in order to observe at least five susceptible individuals (a valid χ^2 test requires that there be at least five individuals in the smallest category).

The resistant lines G 5864, PI 137739, PI 262660, PI 372129, PI 294994, and PI 243781 exhibited different levels of resistance to RWA. The level of resistance exhibited by PI 137739 and by PI 262660 is much lower than that exhibited by G 5864. In fact, actual plant survival of PI 137739 and PI 262660, in terms of eventual plant death, may be close to that shown by the susceptible check Karl 92 (Table 3), yet these lines do not exhibit the characteristic ‘susceptible’ reaction of tight leaf rolling and white streaking. This low level of resistance has been observed repeatedly in our screening tests. Even though low, this level of resistance can be effective against RWA in the field and, in fact, is currently being used in many wheat breeding programs around the world. It is important that caution be taken not to confuse this low level of resistance with the typical susceptible reaction, which is very dis-

Table 3. Reactions of resistant bread wheat lines to Russian wheat aphid and segregation in the F_2 progeny derived by crossing G 5864 to other resistant lines. The susceptible wheat cultivars Karl 92 and Custer were used as checks

Cross	Observed classes of reaction			
	R[a]	M1	M2	S
	– no. of plants observed –			
G 5864 × PI 137739				
G 5864	18			
PI 137739 (*Dn1*)			20	
F_2	350	4	4	
Karl 92 (check)				80
G 5864 × PI 262660				
G 5864	16			
PI 262660 (*Dn2*)			15	
F_2	318	14	21	
Karl 92 (check)				80
G 5864 × PI 372129				
G 5864	20		2	
PI 372129 (*Dn4*)	20			
F_2	362		7	
Karl 92 (check)				80
G 5864 × PI 294994				
G 5864	20			
PI 294994 (*Dn5*)	18		2	
F_2	347		9	
Karl 92 (check)				80
G 5864 × PI 243781				
G 5864	47			
PI 243781 (*Dn6*)	23	16	5	
F_2	255	45	18	
Custer (check)				300

[a] R = highly resistant; flat leaves with isolated chlorotic flecks; M1 = intermediate resistance; loosely rolled leaves with little if any chlorosis; M2 = low resistance; flat leaves with stunted growth, may have chlorosis; S = susceptible; tightly rolled leaves with extensive streaking and chlorosis.

tinctive. If screening tests are not carefully monitored, plants with low levels of resistance may die under severe infestation and then mistakenly be included in the susceptible class. This would result in false conclusions; in this study, if M1 was wrongly classified as R, and M2 wrongly classified as susceptible, then the F_2 data would fit a 3 : 1 ratio.

Resistant lines G 5864, PI 294994, and PI 243781 each exhibited a range of resistance to RWA. This could be due to seed quality and seedling vigor, the expression of minor genes or modifiers, interactions of major gene(s) with environmental factors, contamination in the pollen or seed source, and/or the presence of multiple genotypes in a single accession number. In addition, new gene combinations produced by hybridizing two different resistant genotypes may result in previously unseen rating categories; crossing lines with different levels of resistance and the resulting production of new gene combinations could be expected to produce widely segregating populations that may have individual plants that are difficult to categorize.

In fact, the segregation pattern in each of the F_2 populations developed for testing allelism was not clear due to the range of reaction within the 'resistant' categories (Table 3). However, each screening flat included susceptible check wheats, including the susceptible parents; all showed the typical susceptible reaction, indicating adequate infestation levels and little environmental effect. Due to the reasons discussed above, along with the distinct rolling and streaking reaction of a susceptible plant, analysis of the allelism populations may best be done if based on a (R + M) : S basis. The lack of susceptible plants in the F_2 populations might suggest that the type of resistance manifested in G 5864 and that shown by the other resistant lines were caused by different alleles at the same locus, or that G 5864 shares a gene with each of the other resistant lines.

The presence of different resistant genotypes in a single line (Zhang et al., 1997) could definitely produce the conflicting and confusing results that have been reported in the literature. It also makes it difficult or impossible to compare and synthesize results obtained in different studies. Other RWA-resistant lines studied, besides PI 294994, could also prove to have multiple resistant genotypes with different resistance genes. The primary source for most of the available RWA-resistant germplasm has been the USDA-ARS National Small Grains Collection in Aberdeen, ID. The mission of this facility is to maintain all of the genetic diversity present in the original collections. If the original collections were not done on a single plant basis, the chance for genetic diversity within a single plant introduction is great; this possibility should be addressed in future genetic experiments by assuring that a single true-breeding plant is used for making crosses. It must then be remembered that the results obtained with that particular plant may not apply to all plants within a single accession number.

Additional complications in genetic experiments arise when evaluating different accessions, and crosses between different accessions, because of the different

levels of resistance that may be expressed. Some lines that are currently being used in breeding programs are highly resistant while others are only moderately resistant. Crosses between different resistance sources produce new gene combinations that may give a range of symptom expression that is not covered by previously acceptable rating scales. In addition, different damage rating scales have been used by different researchers to characterize reaction types and classes in the segregating populations (Saidi & Quick, 1996; Elsidaig & Zwer, 1993). If plants are merely divided into 'resistant' and 'susceptible' categories, then intermediate categories may be overlooked and genetic analysis could be limited to a single gene model. This has been the case in several of the studies designed to determine the inheritance of RWA resistance gene(s) present in the resistant lines included in this study. If, in the initial rating, plants are rated in as many categories as are observed, then it could be determined at a later time if the intermediates should actually be included in the 'resistant' class (for example, intermediacy could possibly be caused by environmental interactions). It would then be possible to regroup and reanalyze.

The problems associated with screening for RWA resistance and possible sources of these problems were recently pointed out by Baker et al. (1996). A topcross procedure was suggested to identify the number of genes differentiating two resistant parents. Baker et al. (1996) used this procedure and concluded that PI 137739 and PI 262660 each have a major gene for RWA resistance (*Dn1* and *Dn2*, respectively) and a modifier gene, which might be additive. PI 372129 was shown to have a major gene (*Dn4*) that conferred a high level of resistance. The topcross procedure also indicated that PI 294994 has three genes for RWA resistance (*Dn1*, *Dn2*, and *Dn4*, or alleles of these genes). If it is assumed that G 5864 has two major genes for RWA resistance, as indicated by this study, and that these genes are different from other known resistance genes, then F_2 populations derived from crossing G 5864 with other resistant lines were segregating for between three to five different resistance genes plus a modifier gene. This necessitates the testing of large F_2 populations derived from such crosses in order to detect the minimum number of susceptible plants for a valid χ^2 test. For example, with four major genes differentiating the parents of a resistant $\times$ resistant cross, the size of the F_2 population derived from such a cross should at least include 1280 progeny in order to detect five susceptible plants (the minimum number that should be in the smallest category for a valid χ^2 test). The additional presence of modifier genes (suggested by the results of Marais & Du Toit (1993), Schroeder-Teeter et al. (1994), and Baker et al. (1996)) further increases the size of an acceptable F_2 population. Therefore, one possible reason for the lack of appearance of susceptible plants in F_2 populations involving G 5864 $\times$ resistant lines could be the moderate size of F_2 populations used in this study. Another possible reason could be that G5864 shares resistance gene(s) with each of the other resistance lines. By using the topcross procedure outlined by Baker et al. (1996), and using known homogeneous lines of all resistance sources, it should be possible to estimate the number of resistance genes differentiating G 5864 from other resistant genotypes. It should be noted that none of the previously published allelism reports used the topcross method, and may not have used homogeneous source populations, and so those results may be subject to question.

Among the resistant lines examined, G 5864 showed the highest level of resistance to RWA under our conditions. The inheritance study indicated that resistance in G 5864 was governed by two independent dominant genes with additive gene effects. In addition, this study showed that allelic relationships among RWA resistance genes and the type of gene action involved are not simple. This was evident from the various and complicated reactions exhibited by wheat plants in the segregating populations exposed to RWA. If previous reports concerning the number of resistance genes present in the other resistant lines are correct, then given the high manifestation of resistance observed in G 5864, and given the absence of susceptible plants in the R $\times$ R F_2 populations, it is indicated that RWA resistance in G 5864 is either controlled by different alleles at the same loci as the other resistance genes, or that G 5864 shares a resistance gene with each of the other resistant lines.

Despite the ambiguity in the literature, it is possible to use conventional breeding or molecular techniques, or both, to incorporate the highest level of resistance into adapted wheat cultivars. A wheat genotype with a high level of resistance and acceptable agronomic characteristics would be obtainable if the backcross method is used to transfer resistance genes into susceptible commercial wheats. Although it can be difficult to pyramid resistance genes, it should be easier to select for multiple genes in a single genotype when those genes have additive effects. G 5864 is a spring bread wheat that requires little vernaliza-

tion and matures about a month later than 'Anza', a semidwarf spring wheat cultivar grown in southern California. In a field experiment (Moghaddam et al., 1997) mean values for G 5864 were 91-cm height, 5 spikes/plant, 28.4-g 1000-kernel weight, 5.1-g/plant yield, and 0.25 harvest index, which suggests a typical landrace genotype (Ehdaie et al., 1988; Ehdaie & Waines, 1989). In the same experiment, mean values of these characters for Anza were 82 cm, 5.0 spikes/plant, 44.0 g, 9.7 g/plant, and 0.41, respectively. Also, G 5864 had faster growth and development and was more productive than other resistant lines examined in this study. These characteristics make G 5864 a desirable genotype for use as a donor parent in breeding programs designed to transfer RWA resistance genes into adapted wheat cultivars.

Acknowledgements

Research supported in part by the California Agricultural Exp. Station, the California Wheat Commission, and the University of California, Riverside, Botanic Gardens. We thank J.G. Waines for reading the manuscript.

References

Baker, C.A., J.A. Webster & D.R. Porter, 1992. Characterization of Russian wheat aphid resistance in a hard white spring wheat. Crop Sci 32: 1442–1446.

Baker, C.A., D.R. Porter & J.A. Webster, 1996. Identification of genetic diversity for Russian wheat aphid resistance in wheat. In: Agronomy Abstracts. p. 93. ASA, Indianapolis, IN.

Du Toit, F., 1987. Resistance in wheat (*Triticum aestivum*) to *Diuraphis noxia* (Hemiptera: Aphididae). Cereal Res Commun 15: 175–179.

Du Toit, F., 1988. Another source of Russian wheat aphid (*Diuraphis noxia*) resistance in *Triticum aestivum*. Cereal Res Commun 16: 105–106.

Du Toit, F., 1989. Inheritance of resistance in two *Triticum aestivum* lines to Russian wheat aphid (Homoptera: Aphididae). J Econ Entomol 82: 1251–1253.

Ehdaie, B., J.G. Waines & A.E. Hall, 1988. Differential responses of landrace and improved spring wheat genotypes to stress environments. Crop Sci 28: 838–842.

Ehdaie, B. & J.G. Waines, 1989. Genetic variation, heretibility and path-analysis in landraces of bread wheat from southwestern Iran. Euphytica 41: 183–190.

Elsidaig, A.A. & P.K. Zwer, 1993. Genes for resistance to Russian wheat aphid in PI 294994 wheat. Crop Sci 33: 998–1001.

Marais, F.G. & F. Du Toit, 1993. A monosomic analysis of Russian wheat aphid resistance in the common wheat PI 294994. Plant Breed 111: 246–248.

Meyer, W.L., K.K. Nkongolo, F.B. Peairs & J.S. Quick, 1989. Mechanism of resistance in the wheat line PI 372129 to the Russian wheat aphid. In: D. Baker (Ed.), Proc. 3rd Russian Wheat Aphid Conf., Albuquerque, NM. 25–27 Oct. 1989, p. 23–24. New Mexico State Univ., Las Cruces, NM.

Moghaddam, M., B. Ehdaie & J.G. Waines, 1997. Genetic variation and interrelationships of agronomic characters in landraces of bread wheat from southeastern Iran. Euphytica 95: 361–369.

Nkongolo, K.K., J.S. Quick, A.E. Limin & D.B. Fowler, 1991. Sources and inheritance of resistance to Russian wheat aphid in *Triticum* species amphiploids and *Triticum tauschii*. Can J Plant Sci 71: 703–708.

Quick, J.S., 1989. Results of the first uniform Russian wheat aphid seedling test. In: West. Soc. Crop Sci. Abstracts, p. 21. Bozeman, MT.

Quick, J.S., K.K. Nkongolo, W.L. Meyer, F.B. Peairs & B. Weaver, 1991. Russian wheat aphid reaction and agronomic and quality traits of a resistant wheat. Crop Sci 31: 50–53.

Robinson, J., P.A. Burnett, H.E. Vivar & F. Delgado, 1992. Russian wheat aphid in barley: inheritance of resistance and yield loss. In: W.P. Morrison (Ed.), Proc. 5th Russian Wheat Aphid Conf., Fort Worth, TX, 26–28 Jan. 1992, p. 94–97. Texas Agr. Ext. Serv., Lubbock, TX.

Saidi, A. & J.S. Quick, 1996. Inheritance and allelic relationships among Russian wheat aphid resistance genes in winter wheat. Crop Sci 36: 256–258.

Schroeder-Teeter, S., R.S. Zemetra, D.J. Schotzko, C.M. Smith & M.M. Rafi, 1994. Monosomic analysis of Russian wheat aphid (*Diuraphis noxia*) resistance in *Triticum aestivum* line PI 137739. Euphytica 74: 117–120.

Smith, C.M., D. Schotzko, R.S. Zemetra, E.J. Souza & S. Schroeder-Teeter, 1991. Identification of Russian wheat aphid (Homoptera: Aphididae) resistance in wheat. J Econ Entomol 80: 328–332.

Steel, R.G.D. & J.H. Torrie, 1980. Principles and Procedures of Statistics, 2nd Ed., McGraw-Hill, New York.

Stoetzel, M.B., 1987. Information on and identification of *Diuraphis noxia* and other aphid species colonizing leaves of wheat and barley in the United States. J Econ Entomol 80: 696–704.

Webster, J.A., 1990. Resistance in triticale to the Russian wheat aphid (Homoptera: Aphididae). J Econ Entomol 83: 1091–1095.

Webster, J.A., K.J. Starks & R.L. Burton, 1987. Plant resistance with *Diuraphis noxia* (Homoptera: Aphididae), a new United States wheat pest. J Econ Entomol 80: 944–949.

Zhang, Y., J.S. Quick & S. Liu, 1997. Genetic variation in PI 294994 wheat for resistance to Russian wheat aphid. In: Agronomy Abstracts. ASA, p. 67. Anaheim, CA.